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Object-Use in Free-Ranging White-Faced Capuchins (*Cebus capucinus*) in Costa Rica

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ABSTRACT Chimpanzees and capuchins demonstrate greater varieties and higher rates of tool-use when compared to other non-human primates. Although capuchins have been studied extensively in captivity, data on their tool-using behavior under free-ranging conditions are limited. This is the first long-term field research to systematically study complex object manipulation in capuchins. The aims of this research are 1) to examine the types, rates, and contexts of tool- and object-use in free-ranging capuchins and 2) to determine if free-ranging capuchins' object manipulation behavior is comparable to the behavior exhibited by captive individuals. Data on 3 troops of white-faced capuchins (*Cebus capucinus*) were collected from February 1995 to January 1996 at Palo Verde, Costa Rica. Data were collected using focal animal and ad libitum sampling techniques. Any observed incident of tool-use and object-use was recorded. No tool-use was observed during the 11-month study. Object-use (pound, rub, and fulcrum-use) occurred at a rate of 0.19/hr and made up less than 1% of the monkeys' time (there were no differences among the age/sex classes). The results indicate that free-ranging capuchins do not exhibit the range of tool-using behavior demonstrated by their captive counterparts. This may be the result of differential motivational responses to objects, arboreal lifestyle, absence of adequate tool material, and/or absence of food resources that require extraction involving tool-use. Am J Phys Anthropol 106:311–321, 1998.

The complex manipulation and use of objects were once considered uniquely human behaviors. The use of objects, including both tool-use ["the external employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself" (Beck, 1980: 10)] and object-use (the manipulation and alteration of a detached object relative to a fixed substrate or medium; Parker and Gibson 1977), is now known to occur in species representing almost every group of animals including fish, birds, and mammals (for review see Beck, 1980). Among mammals, research has focused particularly on non-human primates.

Non-human primates have often been singled out from other animals because of their phylogenetic proximity to humans and because of potential unique aspects of their object-using behavior. For example, Parker and Gibson (1977) make a distinction between the "context-specific" (i.e., stereotyped) behavior of non-primate animals and the "intelligent" (non-stereotyped) object manipulation of many primates [however, see Chevalier-Skolnikoff and Liska's (1993)

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study of tool-use in elephants (*Loxodonta africana* and *Elephus maximus*)].

There have been several species-specific studies focusing on non-human primate object manipulation [e.g., *Macaca tonkeana* (Anderson, 1985); *M. silenus* (Westergaard, 1988); *Pan paniscus* (Ingmanson, 1996; Jordan, 1982); *P. troglodytes* (McGrew and Marchant, 1992; Nishida, 1973; Sugiyama et al., 1993); *Papio anubis* (van Lawick-Goodall et al., 1973); *Pongo pygmaeus* (Galdikas, 1982; Russon and Galdikas, 1992; Wright, 1972)], as well as broader studies that have compared object manipulation across several species (e.g., Natale et al., 1988; Torigoe, 1985; Vancatova, 1987). Although several primate species (both monkeys and apes) have been reported to use tools, chimpanzees (*Pan* spp.) and capuchins (*Cebus* spp.) (at least in captivity) show both greater varieties and higher rates of tool-use when compared to all other primates, excluding humans.

In captivity, capuchins demonstrate a propensity for tool-use and will often spontaneously use tools when provided with adequate materials. The types of tool-use reported for captive capuchins include hitting conspecifics with sticks (Cooper and Harlow, 1961, as reported in Visalberghi, 1990); using sticks as probing tools (Anderson and Henneman, 1994; Westergaard and Fragaszy, 1987; Westergaard and Suomi, 1993b; Westergaard et al., 1997); using sponging tools (Westergaard and Fragaszy, 1987; Westergaard et al., 1995); using rocks and wood to pound open hard-shelled nuts (Anderson, 1990; Antinucci and Visalberghi, 1986; Visalberghi, 1988; Visalberghi and Vitale, 1990; Westergaard and Suomi, 1993a,b); throwing stones at targets (Westergaard and Suomi, 1994a); using sticks as levers and as chisel-and-hammers (Jalles-Filho, 1995); using stones and sticks as pestles (Westergaard et al., 1995); modifying bones with rock to make appropriate probing tools (Westergaard and Suomi, 1994c); modifying bamboo to make probing and cutting tools (Westergaard and Suomi, 1995); and modifying stones to make cutting tools (Westergaard, 1995).

The reported rates of tool-use per individual are often very high [for those studies that provide explicit rate information, 1.7 bouts/hr for a variety of spontaneous tool-use with novel objects (Chevalier-Skolnikoff, 1989) and 1.6 bouts/hr with a variety of sponging tools (Westergaard and Fragaszy, 1987)]. However, there are often significant differences among individuals in the amount of tool-use exhibited (i.e., from those that never use tools to those that use tools in almost every trial within the same study group) (Anderson, 1990; Anderson and Henneman, 1994; Antinucci and Visalberghi, 1986; Jalles-Filho, 1995; Visalberghi, 1987, 1988; Fragaszy and Visalberghi, 1990; Westergaard and Fragaszy, 1987; Westergaard and Suomi, 1994b; Westergaard et al., 1995, 1997).

There are several factors that enable capuchins to use tools. First, capuchins are morphologically capable of complex manipulative tasks; they possess a semi-opposable thumb and are capable of both power and precision grips (Costello and Fragaszy, 1988; Westergaard and Suomi, 1997). Second, when compared to other (non-hominoid) species, capuchins demonstrate longer attention spans, greater interest in novel objects, and greater variation in their pattern of exploration, all behaviors that promote object- and tool-use (Glickman and Sroges, 1966; Visalberghi, 1990).

Most of the tool-using behaviors observed in captive capuchins have also been observed in both captive and free-ranging chimpanzees (Chevalier-Skolnikoff, 1989; McGrew, 1992), and are argued to be similar to the tool-using behavior of early hominids (e.g., Kortlandt, 1986; Sussman, 1994). Because chimpanzees and early hominids are phylogenetically distant from capuchins, their possible behavioral convergence in regard to tool-use may be partially explained by ecological factors. For instance, Parker and Gibson (1977) suggest that an omnivorous, highly seasonal diet depending on extractive foraging may have led to tool-use in primates.

Before determining the possible ecological factors that may have led to tool-use in primates, however, an understanding of how both chimpanzees and capuchins use tools under natural conditions is required. Such comparisons are not possible at this time.

Although studies of tool-use in free-ranging chimpanzees have increased recently (e.g., Ingmanson, 1996; McGrew and Marchant, 1992; Sakura and Matsuzawa, 1991; Sugiyama et al., 1993), little is known about object manipulation in free-ranging capuchins.

What is known about object manipulation in free-ranging capuchins comes mainly from anecdotal reports. These anecdotal reports include accounts of free-ranging capuchins hitting a potential snake predator with sticks (in *C. capucinus:* Boinski, 1988; Chapman, 1986), pounding oysters open with pieces of an oyster bed (in *C. apella:* Fernandes, 1991), and pounding hard-shelled fruits and nuts against tree branches (in *C. apella:* Izawa and Mizuno, 1977; Struhsaker and Leland, 1977; Terborgh, 1983), but the rates and true contexts of these behaviors are unknown.

The one free-ranging study to date that systematically examined tool-use in capuchins was conducted by Chevalier-Skolnikoff (1990). The data for her project were collected during a 5-month period (2 consecutive months in 1976 and 3 consecutive months in 1977) on *C. capucinus* in Costa Rica.During her study, Chevalier-Skolnikoff (1990) observed several tool-use events, including poking a conspecific with a stick, probing a hole with a stick, breaking and dropping branches on an individual, and flailing sticks at another.

The research presented here is from the first long-term field study to focus on object manipulation in capuchins. The primary aims of this research are to examine the types, rates, and contexts of tool- and object-use in habituated, free-ranging capuchins, and to determine if free-ranging monkeys' object manipulation behavior is comparable to the behavior exhibited by captive individuals. Although almost all of the captive capuchin studies involve *C. apella* and this study focuses on *C. capucinus,* species differences in object manipulation behavior are not expected. The fact that tool-use has been reported anecdotally in both species (e.g., Boinski, 1988; Fernandes, 1991) and quantitatively in *C. capucinus* under free-ranging conditions supports this assumption. Additionally, because the species included in the genus *Cebus* do not differ dramatically in other behaviors, their use of objects and tools would not be expected to vary significantly either (Fragaszy et al., 1990).

MATERIALS AND METHODS

Study site

The study was conducted at Palo Verde National Park in Northwestern Costa Rica (10° 19′ to 10° 24′ N and 85° 18′ to 85° 25′ W). The park is 13,058 ha in size and is connected to Lomas Barbudal Reserve by a narrow corridor, for a total of 15,337 ha of protected land. Palo Verde experiences 2 distinct seasons: a dry season (December–April) with little to no rain and a wet season (May–November) averaging 1,500 mm of rain. During this study, the area received an abnormal amount of rain (2,700 mm), which caused some local flooding. The primary forest type found in the park is tropical dry forest. Deciduous trees make up 80% of the vegetation. These trees shed their leaves completely during the dry season, allowing for exceptionally good visibility.

Study animals

Three troops of white-faced capuchins (*C. capucinus*) were studied from February 1995 to January 1996: the Station Troop (ST) contained 17 individuals at the end of the study (4 adult males, 4 adult females, and 9 immatures); the Lagoon Troop (LT) contained 21 individuals (4 adult males, 5 adult females, and 12 immatures); and the Water Hole Troop (WHT) contained 20 individuals (5 adult males, 6 adult females, and 9 immatures). Two of the troops (ST and LT) used the same area of the park, a large limestone hill near a 4,000 ha marsh, and their home ranges overlapped extensively. The WHT used an area that experienced a severe burn in 1987, and thus was made up of primarily colonizing species of vegetation (e.g., *Guazuma ulmifolia* and *Acacia* spp.). The WHT's home range included an artesian spring-fed water hole and overlapped slightly with at least one other *Cebus* troop.

Data collection

Data for this study were collected using focal animal and ad libitum sampling tech-

niques (Altmann, 1974). During each 10-min focal session, data on object- and tool-use were collected. In addition, because these behaviors were relatively uncommon, any observed occurrence of object- and tool-use was recorded ad libitum. There was no predetermined list of object manipulation behaviors because of the paucity of information available on this topic for free-ranging capuchins. Therefore, all of the behaviors observed which fit the definitions of tool-use and object-use provided below were recorded, named, and described during the course of the study.

Tool-use. Beck's (1980: 10) definition of tool-use was used during this study; therefore, when an individual was involved in "the external employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself when the user holds or carries the tool during or just prior to use and is responsible for the proper and effective orientation of the tool," it was considered tool-use. One important aspect of tool-use is that both the "object of change" and the "agent of change" (i.e., the tool) are manipulated by the user (Parker and Gibson, 1977). The processing of one object in this way was considered a bout.

Object-use. The definition of object-use used during this study was adapted from Parker and Gibson's (1977) definition of proto tool use. Therefore, any time an individual manipulated (to alter) a detached object relative to a fixed substrate or medium, it was considered object-use. One important difference between object-use and tool-use is that with object-use only the "object of change" is detached and manipulated. Again, the processing of one object in this way was considered a bout.

During the 11-month study, a total of 310 hr of focal data were collected and over 1,000 hr of contact were spent with the monkeys. The focal hours are not distributed equally among the 3 study troops: 234 focal hr were collected from the main study troop (ST) over 11 months; 42 hr were collected from WHT from March 1995 to April 1995; and 34 hr were collected from LT from April 1995 to August 1995.

One behavior often considered tool-use, the breaking and dropping of branches, was not analyzed in this study (e.g., Chevalier-Skolnikoff, 1990). It is a common behavior to capuchins and other primate species, such as howler monkeys (*Alouatta* spp.), spider monkeys (*Ateles* spp.), baboons (*Papio* spp.), macaques (*Macaca* spp.), and colobus monkeys (*Colobus* spp.) (Beck, 1980; Struhsaker, 1975). This behavior is so common in capuchins and occurs in so many different contexts, however, that it is often difficult to determine whether or not the branch-breaking is done "to alter more efficiently the form, position, or condition of another object, another organism, or the user itself" (see the above tool-use definition).

Data analysis

Because of the relative infrequency of object-manipulation behavior, most of the object-manipulation data, including all of the quantified data (i.e., focal-animal data), analyzed in this article come from the main study troop (ST). To determine rates of object-use, I divided the total number of object-use bouts performed by an individual during focal observations by the number of focal data hours collected from that individual. This gave me the number of object-use bouts observed per hour per individual. These data were totaled for each age/sex class. To determine possible differences among age/sex classes in regard to object-use rates, Kruskal-Wallis tests were run using SPSS 6.0. Alpha was set at $P = 0.05$.

To compare and determine the amount of time (i.e., the number of focal minutes in which the behavior occurred) each monkey devoted to object-use, data from the focal samples were analyzed (ad libitum data were not included in this part of the analysis). To determine the amount of time, on average, an individual spent in object-using activities, the total number of focal minutes in which a monkey was observed exhibiting object-use was divided by the total number of minutes that monkey was observed (using the focal-animal technique). This procedure was repeated for each individual in the ST and for each age/sex category. To determine

TABLE 1. Assumed functions of object-use

Assumed function	Type of object-use and objects (species if known) associatd with each function		
	Rub	Pound	Fulcrum
To damage the hard outer coating of certain plants and animals to enable ingestion of the material inside	Snails; duck eggs (*Dendrocygna autumnalis*); fruits (*Cassia grandis, Sterculia apetala, Crescentia cujete,* and *Randia armata*)	Snails; duck eggs (*Dendrocygna autumnalis*); clay wasp hives; sticks; fruits (*Cassia grandis, Randia armata, Pithecellobium dulces, Sideroxylon* spp., *Cocos nucifera, Stemmadenia donnell-smithii, Anona reticulata,* and an unidentified vine)	*Pithecellobium saman* fruits
To soften fruits for ingestion	Unripe *Mangifera indica* fruits	*Psidium guajava* and unripe *Mangifera indica* fruits	—[1]
To process fruits prior to fur rubbing which might increase the activation of certain compounds (for a description of fur rubbing, see Baker, 1996)	*Citrus aurantifolia* fruits	*Citrus aurantifolia* fruits	—[1]
To remove wind-dispersed seeds from fruits	*Luehea candida* fruits	*Luehea candida* fruits	—[1]
To remove noxious or stinging substances from particular plants and animals prior to ingestion	Caterpillars; *Tabebuia ochracea* fruits	*Tabebuia ochracea* fruits	—[1]
To detatch fruits from fruit bunches	—[1]	*Bactris minor* fruits	—[1]

[1] An example to fit the category was not observed.

possible differences in the amount of time devoted to object-use activities among the different age/sex classes (i.e., adult males, adult females, subadults, and juveniles), Kruskal-Wallis tests were run. Statistical significance was again set at the $P = 0.05$ level.

RESULTS

Descriptions of object-use

The monkeys exhibited 3 main types of object-use: rub, pound, and fulcrum-use (described below). All of these could be described as "object-substrate" use in that they involve modifying a detached object using a fixed substrate (i.e., tree branch or rock), and they fit the "customary" and the "spontaneous" levels of object manipulation outlined by McGrew and Marchant (1997) (although their levels dealt strictly with tool-use). There are variable assumed functions for each type of object-use (see Table 1).

Twenty-one different types of identified objects (17 plant and 4 animal species) and 7 unidentified objects were involved in the 161 object-use bouts observed during this study (including both focal and ad libitum data). Four plant species (*Cassia grandis, Citrus aurantifolia, Luehea candida,* and *Randia armata*) were involved in a disproportionate number of bouts (57.8% of the object-use bouts observed) (see Tables 2 and 3). In all cases, the object being modified was detached from the substrate and carried to a location appropriate for modification (e.g., to a large branch in the trees or to a large rock on the ground). Of all of the object-use bouts observed, 65.2% were unimanual and 34.8% were bimanual (see Table 2). The types of grip used by the monkeys during object-use were often impossible to determine because of the field conditions.

Of all the object-use bouts observed, most involved pounding, followed by rubbing, and then fulcrum-use (see Table 3). Motor patterns varied slightly depending on the object being modified, the assumed function of the modification, and the individual involved in the object manipulation. The descriptions below represent general patterns for each type of object-use observed.

TABLE 2. Unimanual vs. bimanual object-use[1]

Object (species if known)	% of bouts		Total no. of bouts observed
	Unimanual	Bimanual	
Annona reticulata	50	50	4
Bactris minor	0	100	4
Cassia grandis	24.1	75.9	29
Caterpillar	20	80	5
Citrus aurantifolia	90.9	9.1	22
Clay wasp hive	100	0	6
Cocos nucifera	100	0	1
Crescentia cujete	50	50	2
Dendrocygna autumnalis (egg)	100	0	3
Luehea candida	100	0	20
Magnifera indica	45.5	54.5	11
Pithecellobium dulces	100	0	1
Pithecellobium saman	0	100	3
Psidium guajava	100	0	1
Randia armata	81.8	18.2	22
Sideroxylon spp.	100	0	3
Snail	75	25	4
Stemmadenia donnell-smithii	100	0	3
Sterculia apetala	33.3	66.7	3
Stick	0	100	4
Tabebuia ochracea	0	100	3
Unidentified object	100	0	7
Total	65.2	34.8	161

[1] The data include information from both focal-animal and ad libitum sampling techniques. Totals include data from all types of object-use observed (i.e., rub, pound, and fulcrum).

TABLE 3. Percent of each type of object-use observed[1]

Object (species if known)	% of bouts			Total no. of bouts
	Rub	Pound	Fulcrum	
Annona reticulata	0	100	0	4
Bactris minor	0	100	0	4
Cassia grandis	3.4	96.6	0	29
Caterpillar	100	0	0	5
Citrus aurantifolia	4.5	95.5	0	22
Clay wasp hive	0	100	0	6
Cocos nucifera	0	100	0	1
Crescentia cujete	50	50	0	2
Dendrocygna autumnalis (egg)	33.3	66.7	0	3
Luehea candida	20	80	0	20
Magnifera indica	27.3	72.7	0	11
Pithecellobium dulces	0	100	0	1
Pithecellobium saman	0	0	100	3
Psidium guajava	0	100	0	1
Randia armata	22.7	77.3	0	22
Sideroxylon spp.	0	100	0	3
Snail	25	75	0	4
Stemmadenia donnell-smithii	0	100	0	3
Sterculia apetala	100	0	0	3
Stick	0	100	0	4
Tabebuia ochracea	33.3	66.7	0	3
Unidentified object	28.6	71.4	0	7
Total	17.4	80.7	1.9	161

[1] The data include information from both focal-animal and ad libitum sampling techniques.

Rub. Broadly this behavior involved an individual sliding an object against a tree branch or rock with either 1 or 2 hands (for the assumed functions of rub, see Table 1). An individual typically rubbed the object forward and backward along a tree branch or rock while in a sitting or crouching position.

In a 2-handed rub, usually both hands gripped the object with a space in between or 1 hand was placed over the hand gripping the object (depending on the size of the object being modified). One rubbing bout usually included an uninterrupted series of 5–6 complete forward and backward movements in which continuous contact between the object and the substrate was maintained. After 1 of these bouts the object was normally picked up with 1 hand and was inspected by the monkey. The whole process may be replicated several more times with the same object or the bout may be terminated after the first object inspection. In a 1-handed rub, the pattern was very similar to what has just been described. One difference is that the hand not touching the object either rested on the branch (if in a sitting position) or was used for support (if in a crouching position). Although they were not quantitatively measured, the speed and distance of the forward and backward motion qualitatively varied among rubbing bouts. This may indicate possible individual variations or variations related to the type of object being modified.

Pound. Broadly, this behavior involved an individual hitting an object against a tree branch or rock with either 1 or 2 hands. In regard to body orientation, 1-handed and most of the 2-handed pounding bouts were similar to what has been described for rubbing; however, instead of the object being moved in a forward and backward motion, it was moved in an upward and downward motion. Each bout normally consisted of a series of the following steps: 5–6 repeated pounds followed by an inspection of the object. Many of the species pounded and the assumed functions of pounding overlap with those of rubbing (see Table 1).

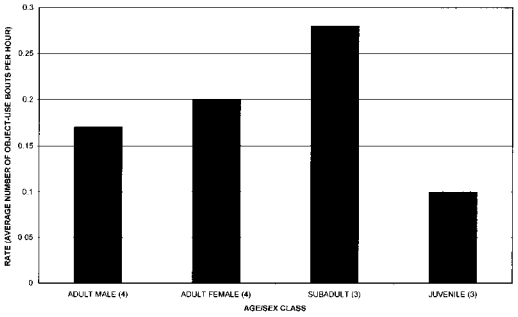

Fig. 1. Rates of object-use among age/sex classes (ST). The bars indicate the average number of object-use bouts observed per hour for each age/sex category. The numbers in parentheses indicate the number of individuals in each age/sex class.

Fulcrum. This type of object-use was less common than either rub or pound. It involved the application of force on an object working against a substrate (which was used as a fulcrum) without moving the object in the process. This type of object-use was only used to break open the fruits of *Pithecellobium saman* to retrieve bruchid beetle larvae (*Merobruchus columbinus*) that live in many of the fruits. A monkey involved in using such a fulcrum positioned itself along a tree branch in the way described for both rubbing and pounding. While either sitting or standing, it placed the fruit perpendicular to the tree branch and applied force downward on the ends of the fruit (which hung over the branch) with 1 hand on each end of the fruit. Since the fruits were normally brittle and easily broken, this process was usually not repeated with the same fruit.

Descriptions of tool-use

The capuchins did not exhibit any behaviors that fit the definition of tool-use provided above. Therefore, the remainder of the Results will deal strictly with object-use.

Rates of object-use

Overall, the monkeys (the ST individuals, excluding infants) exhibited an object-use rate of 0.19/hr (43 object-use bouts during 229.5 hr of observation). There were no significant differences among the age/sex classes in regard to this behavior (Fig. 1).

TABLE 4. Object-use bouts per individual (ST)[1]

Individual	No. of pounding bouts	No. of rubbing bouts	No. of fulcrum-use bouts	Total
AM1	1	0	0	1 (1)
AM2	0	5	0	5 (5)
AM3	1	2	0	3 (1)
AM4	8	1	2	11 (4)
AF1	7	1	0	8 (0)
AF2	3	0	1	4 (0)
AF3	10	1	0	11 (5)
AF4	16	3	0	19 (8)
SF1	5	0	0	5 (2)
SM1	53	1	0	54 (7)
SM2	1	10	0	11 (5)
J1	14	3	0	17 (2)
J2	10	0	0	10 (2)
J3	0	2	0	2 (1)
Total	129	29	3	161 (43)

[1] The number of bouts (for each type of object-use) observed per ST individual is shown. The data include information from both focal and ad libitum sampling techniques. The numbers in parentheses indicate the number of bouts (out of the total number) that were observed during focal samples. AM = adult male; AF = adult female; SF = subadult female; SM = subadult male; J = juvenile.

Two of the 14 troop individuals did not exhibit object-use behaviors during a single focal period, however, every individual (excluding infants) was observed exhibiting at least 1 object-use bout when ad libitum data are included. The number of object-use bouts observed per individual during the study period (when both focal and ad libitum data are considered) ranged from 1 to 54, with an average of 11.5 (see Table 4).

Time spent in object-use activities

Overall, the monkeys (excluding infants) spent 0.4% of the total focal observation time in object-use activities (0.86 hr of object-use during 229.5 hr of observation). Although there were some differences among individuals, there was no significant difference among age/sex classes in regard to the amount of time spent in object-use activities.

DISCUSSION

Although free-ranging capuchins are highly manipulative monkeys, especially in regard to foraging activity (e.g., they often peel bark, probe into tree holes, and break into hollow sticks in search of food), they appear to behave differently from captive capuchins in terms of behavior related to object manipulation. Not a single tool-use

bout (which involved the manipulation of both an "object of change" and an "agent of change") was observed during this 11-month study and the amount of object-use behavior (which involved the manipulation of only an "object of change") was lower than would be predicted from the captive *Cebus* literature. Overall, object-use bouts during this study occurred at a rate of 0.19/hr and made up less than 1% of the monkeys' total time.

The fact that I did not witness a single tool-use event was surprising. It is clear that capuchins have the ability and do exhibit tool-use under free-ranging conditions because of the available field reports (Boinski, 1988; Chevalier-Skolnikoff, 1990; Fernandes, 1991). The differences between the results of this study and the observations of others may indicate that *Cebus* tool-use can vary according to habitat type (and available materials), species, and/or population.

The hammer and anvil use reported for *C. apella* opening oyster shells by Fernandes (1991) involved a group of monkeys living in a mangrove swamp that lacked abundant food resources. The only available quantitative study of object manipulation in this genus, which was conducted by Chevalier-Skolnikoff (1990), involved the same species (*C. capucinus*) and habitat type (tropical dry forest) as reported here. Chevalier-Skolnikoff [using Beck's (1980) definition of tool-use], however, reported seeing several tool-use bouts (5, excluding both the dropping of sticks for reasons discussed above and defecation, in 300 hr of observation). The negative results from the Palo Verde population may indicate a possible population difference or simply demonstrate that this is a rare behavior pattern.

Because no tool-use was observed, it is difficult to compare the results from this study to most of the captive research that has been conducted on this topic; nearly all of the captive literature has strictly examined tool-use and only one, that I am aware of, has discussed object-use behavior quantitatively [although many captive studies do mention that rubbing and pounding are common among capuchins (Antinucci and Visalberghi, 1986; Visalberghi, 1988; Visalberghi and Vitale, 1990)]. The one captive study that considered object-use specifically reports it at a rate of 16 bouts/hr (although their definition of object-use was more inclusive than the one used here, and included such things as pounding and rubbing objects against the enclosure and licking or picking food off of the wall) (Fragaszy and Adams-Curtis, 1991).

In regard to object-use, rubbing, pounding, and fulcrum-use were observed during this study. Rubbing has been observed in many other monkey species (see Torigoe, 1985) and fulcrum-use was a rare object-use behavior in the Palo Verde population. Pounding, which is commonly observed in apes but not in most monkey species, was the most common type of object-use observed during this study. The fact that pounding can be heard and is more likely seen than the other object-use behaviors and that some ad libitum data were used, make the potential differences in the rates of the 3 types of object-use difficult to interpret.

What seems clear at this point is that the rate of capuchin tool-use is much higher under captive than under free-ranging conditions. This pattern is similar to what has been described for 2 ape species: bonobos (*Pan paniscus*) and orangutans (*Pongo pygmaeus*). Bonobos and orangutans are both proficient tool-users in captivity and obviously possess the cognitive abilities necessary for tool-use. For example, bonobos and orangutans have been observed using and making several types of tools under captive conditions including probing tools, sponges, water containers, and modified stone tools (e.g., de Waal, 1997; Jordan, 1982; McGrew, 1992; Toth et al., 1993; Wright, 1972). However, tool-use (as defined here) has never been observed in free-ranging bonobos, and there is only one known report of tool-use in wild orangutans [the use of probing tools (van Schaik et al., 1996)]. There are several possible, not necessarily mutually exclusive, reasons that might explain this pattern. Although the discussion below focuses on capuchins, many of the following potential explanations can also be applied to bonobos and orangutans.

Looking specifically at capuchins, the differences between testing conditions might reflect species differences; almost all of the captive capuchin studies involve *C. apella*,

whereas the 2 quantitative field studies that have examined complex object manipulation in capuchins involve *C. capucinus* (this study; Chevalier-Skolnikof, 1990). However, as discussed earlier, species differences within this genus in regard to object manipulation are not expected (but this assumption will require further testing).

Second, there may be motivational differences between captive and free-ranging monkeys. Captive capuchins may be more motivated simply as a result of the boredom associated with a captive situation; any novel object or potential food source may elicit a heightened interest and response (Fragaszy and Visalberghi, 1990; Visalberghi, 1988). In addition, adequate tool materials may not be readily available to free-ranging animals. This, however, does not seem likely to explain the lack of tool-use observed in the Palo Verde population. Many of the materials provided as potential tools and spontaneously used under captive conditions (e.g., sticks and stones) were plentiful at Palo Verde.

Another possible explanation for the differences in rates may be explained by the amount of time spent on the ground (McGrew, 1992; McGrew and Marchant, 1997; Visalberghi, 1987). Most of the tool-use described in captivity involves capuchins on the ground where stability can be maintained and there is no danger of falling (Anderson, 1990; Anderson and Henneman, 1994; Antinucci and Visalberghi, 1986; Visalberghi, 1987; Visalberghi and Vitale, 1990; Westergaard and Fragaszy, 1987; Westergaard and Suomi, 1993b, 1996). The capuchins only spent approximately 5.4% of their time on the ground during this study (personal data). Captive monkeys are probably, overall, much more likely to spend more time on the ground than free-ranging ones because of the lack of undergrowth and a complete lack of potential predators.

The differences in tool-use rates between captive and free-ranging individuals may also be a result of the potential food resources in an area that would require tool-use to process (de Waal, 1997). Many of the foods that require processing in the captive studies can only be obtained by tool-use and not by using object-substrate use techniques (e.g., Fragaszy and Visalberghi, 1990; Visalberghi and Vitale, 1990). Many researchers involved with captive capuchins report that the monkeys will often first try to open an object by pounding or biting it and will resort to tool-use after the other methods have failed (Anderson, 1990; Antinucci and Visalberghi, 1986; Visalberghi and Vitale, 1990).

Another potential difference between the captive data and the data presented here is related to variations in the rates of tool-use among age/sex classes. Many captive studies report that adult males use tools at higher rates and are more interested in objects than other age/sex classes (e.g., Anderson and Henneman, 1994; Visalberghi, 1987, 1988). This was not supported for object-use behavior in this study where there were no differences among age/sex classes. The higher rates seen in captive adult males may be related to their potential ability to monopolize objects and tools or at least socially inhibit others from using them (Anderson, 1990; Anderson and Henneman, 1994; Fragaszy and Visalberghi, 1990; Jalles-Filho, 1995; Visalberghi, 1988). Such monopolization would be difficult under free-ranging conditions.

CONCLUSIONS

In conclusion, free-ranging capuchins exhibit much less complex object-manipulation behavior than their captive counterparts. This may be the result of differential motivational responses to objects, arboreal lifestyle, absence of adequate tool material, and/or absence of food resources that require extraction involving tool-use. The fact that no tool-use behavior was observed during this study, but has been observed in other free-ranging capuchins, may reflect the rarity of the behavior, species differences, habitat differences, and/or population variations.

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LITERATURE CITED

Altmann J (1974) Observational study of behavior: Sampling methods. Behaviour *49:*227–265.

Anderson JR (1985) Development of tool-use to obtain food in a captive group of *Macaca tonkeana.* J. Hum. Evol. *14:*637–645.

Anderson JR (1990) Use of objects as hammers to open nuts by capuchin monkeys (*Cebus apella*). Folia Primatol. *54:*138–145.

Anderson JR and Henneman MC (1994) Solutions to a tool-use problem in a pair of *Cebus apella*. Mammalia *58:*351–361.

Antinucci F and Visalberghi E (1986) Tool use in *Cebus apella:* A case study. Int. J. Primatol. *7:*351–363.

Baker M (1996) Fur rubbing: Use of medicinal plants by capuchin monkeys (*Cebus capucinus*). Am. J. Primatol. *38:*263–270.

Beck B (1980) Animal Tool Behavior: The Use and Manufacture of Tools by Animals. New York: Garland Press.

Boinski S (1988) Use of a club by a wild white-faced capuchin (*Cebus capucinus*) to attack a venemous snake (*Bothrops asper*). Am. J. Primatol. *14:*177–179.

Chapman CA (1986) Boa constrictor predation and group response in white-faced cebus monkeys. Biotropica *18:*171–172.

Chevalier-Skolnikoff S (1989) Tool use in *Cebus:* Its relation to object manipulation, the brain, and ecological adaptations. Behav. Brain Sci. *12:*610–627.

Chevalier-Skolnikoff S (1990) Tool use by wild cebus monkeys at Santa Rosa National Park, Costa Rica. Primates *31:*375–383.

Chevalier-Skolnikoff S and Liska J (1993) Tool use by wild and captive elephants. Anim. Behav. *46:*209–219.

Costello MB and Fragaszy DM (1988) Prehension in *Cebus* and *Saimiri.* I. Grip type and hand preference. Am. J. Primatol. *15:*235–245.

Fernandes MEB (1991) Tool use and predation of oysters (*Crassostrea rhizophorea*) by the tufted capuchin, *Cebus apella apella,* in brackish water mangrove swamp. Primates *32:*529–531.

Fragaszy DM and Adams-Curtis LE (1991) Generative aspects of manipulation in tufted capuchin monkeys (*Cebus apella*). J. Comp. Psychol. *105:*387–397.

Fragaszy DM and Visalberghi E (1990) Social processes affecting the appearance of innovative behaviors in capuchin monkeys. Folia Primatol. *54:*155–165.

Fragaszy DM, Visalberghi E, and Robinson JG (1990) Variability and adaptability in the genus *Cebus.* Folia Primatol. *54:*114–118.

Galdikas BMF (1982) Orangutan tool-use at Tanjung Puting Reserve, Central Indonesian Borneo. J. Hum. Evol. *10:*19–33.

Glickman S and Sroges R (1966) Curiosity in zoo animals. Behaviour *26:*151–188.

Ingmanson EJ (1996) Tool-using behavior in wild *Pan paniscus:* Social and ecological considerations. In AE Russon, KA Bard, and ST Parker (eds.): Reaching Into Thought: The Minds of the Great Apes. Cambridge: Cambridge University Press, pp. 190–210.

Izawa K and Mizuno A (1977) Palm-fruit cracking behavior of wild black-capped capuchin (*Cebus apella*). Primates *18:*773–792.

Jalles-Filho E (1995) Manipulative propensity and tool use in capuchin monkeys. Curr. Anthropol. *36:*664–667.

Jordan C (1982) Object manipulation and tool-use in captive pygmy chimpanzees (*Pan paniscus*). J. Hum. Evol. *11:*35–39.

Kortlandt A (1986) The use of stone tools by wild-living chimpanzees and the earliest hominids. J. Hum. Evol. *15:*77–132.

McGrew WC (1992) Chimpanzee Material Culture: Implications for Human Evolution. Cambridge: Cambridge University Press.

McGrew WC and Marchant LF (1992) Chimpanzees, tools, and termites: Hand preference or handedness? Curr. Anthropol. *33:*114–119.

McGrew WC and Marchant LF (1997) Using the tools at hand: Manual laterality and elementary technology in *Cebus* spp. and *Pan* spp. Int. J. Primatol. *18:*787–810.

Natale F, Poti P, and Spinozzi G (1988) Development of tool-use in a macaque and a gorilla. Primates *29:*413–416.

Nishida T (1973) The ant-gathering behaviour by the use of tools among wild chimpanzees of the Mahali Mountains. J. Hum. Evol. *2:*357–370.

Parker S and Gibson K (1977) Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in cebus monkeys and great apes. J. Hum. Evol. *6:*623–641.

Russon AE and Galdikas BMF (1992) Imitation in ex-captive orangutans (*Pongo pygmaeus*). J. Comp. Psychol. *107:*147–161.

Sakura O and Matsuzawa T (1991) Flexibility of wild chimpanzee nut-cracking behavior using stone hammers and anvils: An experimental analysis. Ethology *87:*237–248.

Struhsaker TT (1975) The Red Colobus Monkey. Chicago: University of Chicago Press.

Struhsaker T and Leland L (1977) Palm-nut smashing by *Cebus apella* in Columbia. Biotropica *9:*124–126.

Sugiyama Y, Fushimi T, Sakura O, and Matsuzawa T (1993) Hand preference and tool use in wild chimpanzees. Primates *34:*151–159.

Sussman RL (1994) Fossil evidence for early hominid tool use. Science *265:*1570–1573.

Terborgh J (1983) Five New World Primates: A Study in Comparative Ecology. Princeton, NJ: Princeton University Press.

Torigoe T (1985) Comparison of object manipulation among 74 species of non-human primates. Primates *26:*182–194.

Toth N, Schick KD, Savage-Rumbaugh ES, Sevcik RA, and Rumbaugh DM (1993) Pan the tool-maker: Investigations into the stone tool-making and tool-using capabilities of a bonobo (*Pan paniscus*). J. Arch. Sci. *20:*81–91.

Vancatova MA (1987) Experimental study of tool behavior in monkeys and apes (abstract). Int. J. Primatol. *8:*508.

van Lawick-Goodall J, van Lawick H, and Packer C (1973) Tool-use in free-living baboons in the Gombe National Park, Tanzania. Nature *241:*212–213.

van Schaik CP, Fox EA, and Sitompul AF (1996) Manufacture and use of tools in wild Sumatran orangutans: Implications for human evolution. Naturwissenschaften *83:*186–188.

Visalberghi E (1987) Acquisition of nut-cracking behaviour by 2 capuchin monkeys (*Cebus apella*). Folia Primatol. *49:*168–181.

Visalberghi E (1988) Responsiveness to objects in two social groups of tufted capuchin monkeys (*Cebus apella*). Am. J. Primatol. *15:*349–360.

Visalberghi E (1990) Tool use in *Cebus.* Folia Primatol. *54:*146–154.

Visalberghi E and Vitale AF (1990) Coated nuts as an enrichment device to elicit tool use in tufted capuchins (*Cebus apella*). Zoo Biol. *9:*65–71.

de Waal F (1997) Bonobo: The Forgotten Ape. Berkeley: University of Berkeley Press.

Westergaard GC (1988) Lion-tailed macaques (*Macaca silenus*) manufacture and use tools. J. Comp. Psychol. *102:*152–159.

Westergaard GC (1995) The stone-tool technology of capuchin monkeys: Possible implications for the evolution of symbolic communication in hominids. World Arch. *27:*1–9.

Westergaard GC and Fragaszy DM (1987) The manufacture and use of tools by capuchin monkeys (*Cebus apella*). J. Comp. Psychol. *101:*159–168.

Westergaard GC and Suomi SJ (1993a) Use of a tool-set by capuchin monkeys (*Cebus apella*). Primates *34:*459–462.

Westergaard GC and Suomi SJ (1993b) Hand preference in the use of nut-cracking tools by tufted capuchin monkeys (*Cebus apella*). Folia Primatol. *61:*38–42.

Westergaard GC and Suomi SJ (1994a) Aimed throwing of stones by tufted capuchin monkeys (*Cebus apella*). Hum. Evol. *9:*323–329.

Westergaard GC and Suomi SJ (1994b) The use and modification of bone tools by capuchin monkeys. Curr. Anthropol. *35:*75–77.

Westergaard GC and Suomi SJ (1994c) Asymmetrical manipulation in the use of tools by tufted capuchin monkeys (*Cebus apella*). Folia Primatol. *63:*96–98.

Westergaard GC and Suomi SJ (1995) The manufacture and use of bamboo tools by monkeys: Possible implications for the development of material culture among East Asian hominids. J. Archaeol. Sci. *22:*677–681.

Westergaard GC and Suomi SJ (1996) Hand preference for stone artefact production and tool-use by monkeys: Possible implications for the evolution of right-handedness in hominids. J. Hum. Evol. *30:*291–298.

Westergaard GC and Suomi SJ (1997) Capuchin monkey (*Cebus apella*) grips for the use of stone tools. Am. J. Phys. Anthropol. *103:*131–135.

Westergaard GC, Greene JA, Babitz MA, and Suomi SJ (1995) Pestle use and modification by tufted capuchins (*Cebus apella*). Int. J. Primatol. *16:*643–651.

Westergaard GC, Lundquist AL, Kuhn HE, and Suomi SJ (1997) Ant-gathering with tools by captive tufted capuchins (*Cebus apella*). Int. J. Primatol. *18:*95–103.

Wright RVA (1972) Imitative learning of a flaked stone technology—The case of an orangutan. Mankind *8:*296–306.